TYPE SPECIMENS OF THE GENUS *FENESTELLA* FROM THE LOWER CARBONIFEROUS OF GREAT BRITAIN

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ABSTRACT. The morphology and systematic position of the bryozoan genus *Fenestella* Lonsdale are briefly discussed. Phillips's species of the genus are referred to a variety of genera or declared *nomina dubia*; M'Coy's species are redescribed and a new genus *Parafenestella* erected to contain one of them; two of R. Etheridge junior's species are redescribed, and figured for the first time.

IN recent years extensive work on the fenestrate bryozoan faunas of the Russian and North American Upper Palaeozoic successions has indicated the desirability of distinguishing, in the light of modern techniques, the type specimens on which early specific descriptions were based. The original authors gave, in many cases, only brief descriptions of their material, with inadequate and often inaccurate drawings, or even composite reconstructions. The more commonly occurring British Carboniferous fenestellid species have therefore been difficult to identify with precision, and incomplete knowledge has led not only to misidentifications but to the development of two almost separate lists of names (Russian and North American), while no valid redescriptions of British types have been available as a common comparative standard. The situation has been made worse by the nature of the fossil remains themselves, since fragments of reticulate fronds tend to have a close superficial resemblance.

An attempt was made towards the end of the last century by Shrubsole (1879, 1881) to regularize the position as it then stood, by lumping together many of Phillips's and M'Coy's species and allowing only five 'good' species to persist, but it is not possible to agree with many of Shrubsole's somewhat sweeping conclusions. Most British workers meanwhile solved the problem of naming fenestellid fronds either by applying one or other of Phillips's or M'Coy's names more or less at random, or by recording all remains indiscriminately as *Fenestella sp.*, or by ignoring them altogether. The main effect of these methods has been to render useless, from the systematic stratigraphic point of view, almost all references to species of *Fenestella* in British literature (with the notable exception of Oakley (1948) referring to Malayan material). But the practice led also, though indirectly, to the recognition of *Fenestella plebeia* M'Coy, a wide-ranging form, as the 'accepted type' of the genus *Fenestella* (see, for an example of this usage, Ulrich 1890).

The lack of a definitely described and well-understood type species for the genus, and additional taxonomic difficulties relating to the use of the name *Fenestella*, led Bassler (1935) to re-introduce the genus *Fenestrellina* d'Orbigny 1849, while retaining as the 'accepted genotype' *F. plebeia* (M'Coy). This departure was challenged by Condra and Elias (1941), who applied to the International Commission for Zoological Nomenclature for a suspension of the Rules of Priority in order to retain the name *Fenestella* for the bryozoan genus. A discussion of the position regarding the real type species of the genus has

[Palaeontology, Vol. 4, Part 2, 1961, pp. 221–42, pls. 24–27.]

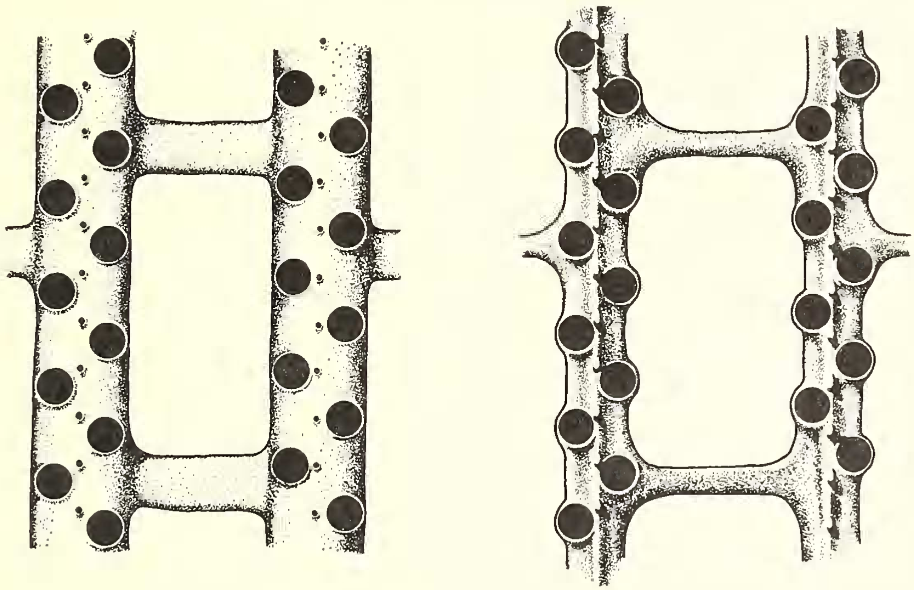
been published by Elias (1956), in relation to *Fenestella subantiqua* d'Orbigny, and this has been criticized by Spjeldnaes (1957). As the matter remains *sub judice* it will be convenient here simply to redescribe the available type material. A summary of the taxonomy of *Fenestella* Lonsdale is contained in Condra and Elias (1944), and an attempt has been made by the same workers (Elias and Condra, 1957) to subdivide and group the known North American Carboniferous species.

MORPHOLOGY OF *FENESTELLA*

The structure of the reticulate fronds of *Fenestella* was first described in detail by Ulrich (1890), and since then many Russian workers (Nekhoroshev, Shulga-Nesterenko, Nikiforova, and others) and Americans, notably Cumings, Condra, and Elias, have contributed to an understanding of the morphological variations within the family. The microstructure is well summarized by Elias (1956, p. 323). Different workers have naturally placed different amounts of emphasis on the various skeletal elements in the process of recognizing and defining species, subspecies, and varieties. Some palaeontologists (e.g. Nekhoroshev 1932; Shulga-Nesterenko 1949*b*) have used the microstructure of the branches and dissepiments as a basis for intra- and inter-specific determinations. However, apart from the shape of the zooecial chambers, this refinement is not considered useful here (cf. Elias and Condra 1957, p. 59).

The desirability of employing a standard biometric usage in measuring mesh dimensions has been stressed by Condra and Elias (1944, p. 54), and it is the counting method used by these authors that should be employed in all descriptions of bryozoan meshes or other similar repetitive structures. This method, the simplest possible, is applicable to all the counts normally needed (of branches, dissepiments, zooecial apertures, and carinal nodes per unit length) and merely requires the count to begin *at zero* and to start and finish at similar structural feature-points. It must be appreciated, however, that the simple record of such a so-called 'micrometric formula' can lead to the confusing of widely differing meshes, if the immediately visible amount of biometric information falls below the minimum required for accurate unambiguous specific determination. Text-fig. 1 shows two obviously different meshes having the same 'micrometric formula'.

Because the organism originated effectively in a point, from which branches radiate (Cumings 1905), no fenestellid mesh retains constant dimensions or proportions over the whole zoarial surface, and the departure from a mean value in any direction is naturally greatest at the base, nearest to the point of origin, in the region of the earliest, immature, most rapidly developing part of the structure. However, variation does occur within the mature or adult mesh region, and it is probable that study of complete specimens would show that the amount of variability itself varies systematically between species or species groups. It might seem necessary, therefore, in descriptive work on the *Fenestellidae*, to obtain as close an approximation as possible to the real range of mesh variation. Condra and Elias (1944), working primarily on the large, well-preserved fenestelloid fronds of *Archimedes*, indicate the position on the zoarial expansion at which each set of measurements was taken. It has not been possible to do this with the material available, which does not include complete or even nearly complete zoaria. Furthermore, in most fenestellid fronds, major variation in mesh dimensions only occurs where several branches divide within a small area, or where the zoarial surface departs widely from a plane, as for example where a fold or wrinkle is developed, especially near the outer edge. Small fragments of zoaria in clastic limestones or shales are nearly always planar, and it is usually possible to avoid, in making mesh counts, regions of abnormally concentrated mesh division. Finally, if total-variation ranges are used when comparing specimens in specific identification, the overlap in range makes it difficult to make satisfactorily objective determinations. It is only by using the narrower variation-range of the mature (or 'stabilized') undistorted mesh that 'good' differentiations can be made. There remains also a possible source of error in the structural distortions imposed by secondary processes working within the rock-matrix. In such cases the mesh may be stretched or compressed in some preferred direction, or the skeletal elements may be thickened by secondarily deposited material or by recrystallization.



TEXT-FIG. 1. Fenestellid meshes with similar 'micrometric formulae' but different gross characters. Notional magnification $\times 75$.

Whatever measurements are made, their value in taxonomy differs according to their relevance to the dimensions of the colony or the dimensions of the individual zooecial chamber. The counts of branches and dissepiments refer to the size and variability of the whole zoarium, while those of zooecial chambers and carinal nodes refer to the distribution-density of the zooids themselves, or related structures. The distribution of the carinal nodes, structures possibly homologous with the acanthopores of the Trepostomata, has in the past often been ignored in published descriptions, but is here considered to be of great systematic importance. In this connexion Elias and Condra state (1957, p. 19):

'Likharev's observation that the carinal spines have the same microstructure as the inner skeleton around the zooecia and as that of the dissepiments is in harmony with the conclusion of Cumings that the carinal spines are part of the primary skeleton or colonial plexus. . . .'

As might be expected, counts of the morphological elements on or in the branches show a much greater stability than the gross zoarial characters, which are more easily affected by simple mechanical distortion, whether this occurs during life or after burial. It is, however, unfortunate that the carinal nodes are easily removed by erosion, and this may account for the absence of reference to carinal nodes in many published diagnoses. Genuine cases of nodeless keels in fenestellid fronds are thought to be rather rare, and any departure from the 'normal' carinal condition, with a single regular row of nodes, is considered to be of primary taxonomic significance. Thus the appearance of a double row of alternating nodes, and the appearance of dissepimental nodes, should be regarded as of generic discriminatory value. This has already been recognized by Crockford (1944, p. 172) in establishing the genus *Minilya* (*Minilia* of Elias and Condra, 1957) for fenestellids with two rows of carinal nodes, and I erect the genus *Parafenestella* for the case with dissepimental nodes.

Comparison of fenestellid material. The very large number of described species of *Fenestella*—over 400, according to Elias and Condra—and the superficial similarity of mesh structure shown by them all, make it useful to devise some way of guarding against the kind of overlap in identification that has clearly operated in the past to proliferate specific names. The meshwork 'micrometric formula' of species of *Fenestella* allows a preliminary sifting of possible correlatives, so that the element of subjective evaluation operates over an initially restricted field. Thus, in identifying a specimen, comparisons are made only with those species known to have a similar micrometric formula, and the final assignment is made by reference to characters like branch thickness, zooecial base-shape, surface ornamentation, and so on.

It has been found that this preliminary sifting can best be done by using a simple punched-card system to record the micrometric formulae of adequately described species. The formula for the specimen to be identified is 'fed-in' to the card-pack, and the eventual 'fall-out' contains all the species with comparable mesh dimensions. Thus, for example, the punched-card system using the micrometric formula with the conventional arrangement of counts produces the following information.

	Branches in 10 mm.	*Dissepiments in 10 mm.*	*Zooecia in 5 mm.*	*Carinal nodes in 5 mm.*
Species studied	12–18	9–10	17–18	19–22
Fall-out of punched cards for comparison:				
F. lahuseni Stuck	15–16	9–10	17–18	19–22
F. plebeia M'Coy	15–23	9–10	17–20	10–20
F. oculata M'Coy	12–18	8–12	15–17	18–24

The field for comparison is reduced by this method to a size in which the application of more subjective tests can proceed without the danger of missing a known form within the observed mesh dimensions.

SYSTEMATIC DESCRIPTIONS

The material described is in three collections, the National Museum of Ireland, Dublin (specimens labelled NMD), the Geological Survey of Great Britain (specimens labelled GS), and the Sedgwick Museum, Cambridge (specimens labelled SM).

Preliminary note on Phillips's species of Retepora. The following have commonly been referred to in the literature under *Fenestella*:

Retepora ('*Fenestella*') *membranacea* Phillips 1836
Retepora ('*Fenestella*') *laxa* Phillips 1836
Retepora ('*Fenestella*') *pluma* Phillips 1836
Retepora ('*Fenestella*') *flabellata* Phillips 1836
Retepora ('*Fenestella*') *tenuifila* Phillips 1836
Retepora ('*Fenestella*') *undulata* Phillips 1836
Retepora ('*Fenestella*') *nodulosa* Phillips 1836
Retepora ('*Fenestella*') *flustriformis* Phillips 1836
Retepora ('*Fenestella*') *irregularis* Phillips 1836

Discussion. All these species were assigned by Phillips to the genus *Retepora*. Some of the names have been quoted uncritically as members of the genus *Fenestella* by later authors, beginning with Portlock (1843), so that certain of them have become embedded in the literature. So far as I know, none of Phillips's material now exists, and to be certain of the validity of some of M'Coy's 1844 species it is necessary to decide whether Phillips's descriptions and illustrations are complete and accurate enough to serve as bases for practically useful diagnoses. So far as concerns the species variously referred during the last hundred years to *Fenestella* Lonsdale, as listed above, Phillips's descriptions are almost useless, since they give almost no structural dimensions, and only a few numerical quantities (such as the number of zooecial apertures to a fenestrule) can be extracted reliably from the figures. In only one case, that of *Fenestella polyporata* (Phillips), discussed below, are the zoarial characters distinctive enough to make it clear which of the known species of *Fenestella* Phillips was dealing with. Phillips's remaining fenestellid species are therefore assigned as follows:

Retepora membranacea: almost certainly not a species of *Fenestella*; probably referable to either *Semicoscinium* Prout, or *Isotrypa* Hall.

Retepora laxa: should be referred to *Polypora* M'Coy.

Retepora pluma: should be referred to *Penniretepora* d'Orbigny, and has, in fact, been designated by Bassler (1953) as the type species of that genus.

Retepora flabellata, *R. tenuifila*, *R. undulata*, *R. nodulosa*, *R. flustriformis*, and *R. irregularis*: although probably referable to *Fenestella*, and discussed twice in this sense by Shrubsole (1879, 1881), these must be discarded as incompletely described. Unless and until the type material is found they are therefore declared *nomina dubia*. This setting aside of *R. irregularis* Phillips, subsequently referred to by various authors as *Fenestella irregularis* (Phillips), as of uncertain systematic position, validates *F. irregularis* Nekhoroshev 1932, which in turn has priority over *F. irregularis* McNair 1942.

Order CRYPTOSTOMATA Shrubsole and Vine 1882
Family FENESTELLIDAE King 1850
Genus FENESTELLA Lonsdale 1839

Fenestella plebeia M'Coy 1844

Plate 24, figs. 1–3

Fenestella plebeia M'Coy 1844, p. 203.
Fenestella ejuncida M'Coy 1844, p. 201.
Fenestella plebeia M'Coy; d'Orbigny 1850, p. 152.
Fenestella plebeia M'Coy; Meek 1872, p. 153.
Fenestella plebeia M'Coy; de Koninck 1876, p. 171.
Fenestella plebeia M'Coy; Shrubsole 1879, p. 278.
Fenestella plebeia M'Coy; Shrubsole 1881, p. 179.
Fenestella plebeia M'Coy; Stuckenberg 1888, p. 52.
Fenestella plebeia M'Coy; Stuckenberg 1895, p. 138.
Fenestella plebeja M'Coy; Nikiforova 1933*b*, p. 10.
Fenestella plebeja M'Coy; Prantl 1934, p. 4.
Fenestella aff. *plebeia* M'Coy; Oakley 1948, p. 89.

M'Coy's description: 'Flat, expanded, fan-shaped; interstices thick; fenestrules equal, rectangular, from two to three times as long as wide; width equal to that of the interstices; dissepiments thin, regular; pores four or five to the length of a fenestrule; reverse minutely granulated, and very coarsely sulcated longitudinally.'

Material:

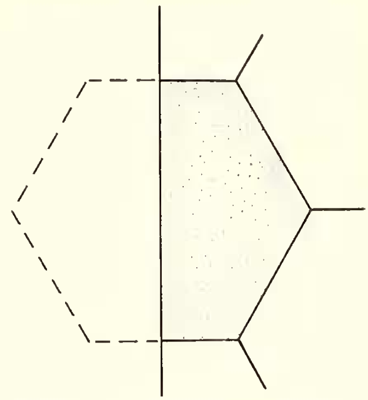
1. Holotype NMD XXIX. 3 from 'Carboniferous Slate', Killybrone, Killala, Eire: probably Upper Tournaisian or Lower Viséan.
2. Homeotype SM E. 5231 from 'Carboniferous Limestone', Kildare, Eire: probably Viséan.
3. Homeotype SM E. 12990 from 'Carboniferous Limestone', Dalry, Scotland: probably Viséan.
4. Homeotype SM E. 17840 from 'Carboniferous Limestone', Dalry, Scotland: probably Viséan.
5. Homeotype NMD XXVIII. 11 from 'Upper Limestone', Black Lion, Enniskillen, Northern Ireland: labelled *Fenestella ejuncida*: probably Viséan.

Micrometric formulae:

Holotype	17–20	8–10	17–20	?
Homeotypes	15–18	8–10	17–20	10–20
F. aff. *plebeia* M'Coy; Oakley 1948 .	18	8–9	18–20	?
F. aff. *plebeja* [*sic*] M'Coy; Prantl 1934 .	16	9–10	?	?

Description. So far as can be made out from fragments, the largest of which measures 50×60 mm., the zoarium is a slightly flexuous fan-shaped, conical or cup-shaped expanded mesh, of subparallel branches joined by short transverse dissepiments. Branches rather slender to moderately robust (ratio of branch-width to fenestrule-width varies from about 1 : 1 to 1 : 2). Branch-width in stabilized part of zoarium 0·12–0·24 mm. (average 0·18 mm.). Obverse smooth, with distinct, rounded, nodiferous carina. Carinal nodes rounded, with slightly elliptical bases, regularly disposed. Reverse rounded, finely striated, with a row of small granules along the axis. Expansion of the zoarium occurs by irregularly spaced symmetrical bifurcation of the branches, more frequent proximally, where it occurs at intervals of about 10 mm. along the branches. The branches are thickwalled tubes longitudinally divided by a regularly zigzag septum set normal to the general plane of the zoarial expansion. The two secondary tubes thus formed are in turn regularly subdivided by transverse walls into rows of box- or coffin-shaped zooecial cells or chambers, the cells of the row on one side of the median septum alternating with those of the row on the other side. In sections in the plane of the zoarial expansion the form of the zooecial chambers (the 'zooecial bases') is subpentagonal or 'hemi-hexagonal' (text-fig. 2). In transverse sections, in which the median septum is seen dividing the branches internally, the inner wall of the zooecial chambers is seen to be ribbed externally, so that the ribs appear as sharp projections of the main skeletal material into the sclerenchymal envelope.

The dissepiments are subcylindrical or flat rod-shaped, rather narrow compared with the branches, of which they are usually little more than half the width, i.e. 0·10 mm. for a branch-width of 0·18 mm. The sclerenchymal outer tissue of the dissepiments is striated parallel to the main axis of the dissepiment. Where the dissepiments join the branches they widen, and the branches also show a slight corresponding bulge. Because of the difference in thickness (or width) the dissepiments are slightly depressed below the general branch-surface level on both sides of the zoarium. The fenestrules are regularly quadrate, coffin-shaped, or subelliptical, depending on their position in the zoarium and relation to points of branch-bifurcation. The numerical density of fenestrules along and across the zoarium corresponds to that of the dissepiments and branches. The zooecial chambers are arranged regularly in two alternating rows in the branches, the rows separated internally by the median septum and externally by the carina. Each chamber is itself partially subdivided by hemisepta, and is provided with a circular aperture on the upper, slightly inclined surface of the branch alongside the carina. In unweathered specimens the zooecial apertures have a thickened margin or peristome. The disposition of the zooecial apertures along the branch is regular, unaffected by the joining-points of the dissepiments, with four or five apertures lying along the side of a fenestrule. When the peristomes are preserved they protrude slightly into the fenestrule, producing a 'beaded' effect.



TEXT-FIG. 2. The 'hemi-hexagonal' shape of zooecial bases in *Fenestella plebeia* M'Coy and other fenestellid meshes.

Discussion. M'Coy's specimen is unsatisfactory for detailed study. It is a badly preserved impression of the reverse of a zoarial fragment in which only at the extreme proximal end are a few relics of the internal structure preserved. The holotype of M'Coy's *F. ejuncida*, here considered conspecific with *F. plebeia*, is a comparatively well-preserved fragment, but also shows only the reverse. The type-locality for *F. plebeia* is a roadside exposure one mile north-west of Kıllala, almost exactly 300 yards east-north-east of triangulation-mark 163, which is figured above the 'a' in Mullaghorn on one-inch map sheet 53. It is almost completely overgrown, and I found there only a few badly preserved fragments, none of them suitable for description as topotype material. Nevertheless, it has been possible to determine M'Coy's intentions in his description and from the holotype, and enough other material is available to reinforce this evidence and so to arrive at a reasonably clear diagnosis.

Occurrence. *F. plebeia* seems to be among the most common fenestellid species in the British Lower Carboniferous (Dinantian series). The dimensions of the mesh and the shape and density of the zooecial chambers remain remarkably constant from the earliest Tournaisian to the latest Viséan examples, but there appears to be a progressive change in the number of carinal nodes, from about 8 in 5 mm. at low Tournaisian horizons, to 18 or 20 towards the top of the Viséan. Further work is needed to establish this development: in any case, since the function (if any) of the carinal nodes and their relation both to the zooecia and the zoarium is unknown, and since the main mesh-dimensions seem to remain constant, it is not reasonable to attempt any subdivision of the species at this time. Many attributions to *F. plebeia* must be regarded as doubtful until the material has been compared with types described here. Conversely, it is likely that examples of *F. plebeia* will be found included under other names. The important North American Mississippian species-group of which *F. rudis* Ulrich is typical (Elias 1937) may well be referable in part to *F. plebeia*. Elias (1943) has recorded *F. plebeia* from Mississippian formations, and F. Kaisin junior (1942, p. 104, pl. vi, fig. 1; not pl. v, as quoted in the text) ascribes to *F.* aff. *rudis* Ulrich specimens from the Belgian Tournaisian having micrometric formulae (16–18 | 9–11 || 20–21 | 14–16) within the limits appropriate to *F. plebeia*. Until corrected identifications have been made in the light of the present redescription it is not possible to draw reliable conclusions as to the stratigraphic range or geographic distribution of *F. plebeia*.

The type species of Fenestella *Lonsdale*. The question arises whether *Fenestella plebeia* M'Coy 1844 should be put forward as the type species of *Fenestella* Lonsdale. Confusion in this matter stems from three causes. First, the type species of *Fenestella* Lonsdale 1839 should be *Gorgonia antiqua* Goldfuss 1829 ('*Gorgonia flabellata, ramis tetragonis, ramulis teretibus reticulatum coniunctis, cortice tenui, osculis lateralibus uniserialibus remotiusculis*') as selected by King in 1850, but the holotype of this species is lost (Toots, 1951) and unrecognizable from the published description and figures (Goldfuss 1826–44, p. 99, pl. xxxvi, fig. 3). Secondly, *Fenestella* Lonsdale for a bryozoan is a junior homonym of *Fenestella* Bolten 1798 for a molluscan. It should be noted, as Spjeldnaes (1957) does, that *both* these names were changed, possibly by misprinting, to *Fenestrella* (Bolten's by Gray in 1848, and Lonsdale's by d'Orbigny in 1850). Thirdly, a practice has arisen, apparently started by Ulrich in 1890, of taking, without formality, *Fenestella plebeia* M'Coy 1844 as the 'accepted type' of the genus, *faute de mieux*, the holotype of the real type species being lost.

In recent decades several authors, aware of the unsatisfactory situation, have used the name *Fenestrellina* for fenestellids formerly included in *Fenestella*, but, as Elias (1956) points out, *Fenestrellina* d'Orbigny 1849 has irregularly spaced dissepiments. Furthermore, Bassler (1953) now regards both *Fenestella* and *Fenestrellina* as morphologically distinct and valid genera. The situation has been still further complicated by the redescription by Elias (1956) of *Fenestella subantiqua* (d'Orbigny), and the designation of this species as the 'genotype', despite Toots's (1951) demonstration of the technical impropriety of this action. In any case, as Spjeldnaes indicates, *Fenestella patula* M'Coy 1850, regarded by Elias as conspecific with *F. subantiqua* (d'Orbigny), should take precedence, and would then become the new type species of *Fenestella*.

It may be useful, in the meantime, to place on record the reasons why *F. plebeia* cannot, without a special decision of the International Commission, be taken as the valid type species:

1. Because it was not an 'included species', and is therefore not eligible for selection as the type species. (Even *Gorgonia antiqua* Goldfuss, which was referred to *F.*

plebeia by Shrubsole (1880), was only doubtfully referred to *Fenestella* by Lonsdale, and is also therefore not directly eligible for selection.)

2. Because *Fenestella antiqua* Lonsdale was validly selected as type species of *Fenestella* Lonsdale by King (1849).

Fenestella hemispherica M'Coy 1844

Plate 24, fig. 4

Fenestella hemispherica M'Coy 1844, p. 202.

M'Coy's description. 'Hemispherical, cup-shaped; interstices and dissepiments exceedingly minute; interstices thin, sharply carinated, reverse longitudinally striated; dissepiments one-fourth the thickness of the interstices; fenestrules rectangular, wider than the interstices, and somewhat longer than wide; pores small, twice their diameter apart, with raised margins which do not indent the edge; about three pores to the length of a fenestrule; . . . about seven interstices in one line.'

Material:

1. Holotype NMD XXIX. 4 from 'Carboniferous Lower Limestone', Little Island, Cork, Eire: probably Tournaisian-Viséan boundary.
2. Homeotype SM E. 17841 from 'Carboniferous Limestone' Easky, Sligo, Eire: probably low Viséan.

Micrometric formulae:

1. Holotype . .	$21\frac{1}{2}$–27 (av. $22\frac{1}{2}$)	12–15	20	12
2. Homeotype . .	20–24	13–15	20–21	10–12

Description. The holotype of *F. hemispherica* is the only specimen in M'Coy's material that shows the form of the zoarium, but, unfortunately, extensive recrystallization of both calcareous skeletal material and matrix has almost completely obscured the fine structural details, particularly the zooecial apertures and carinal nodes.

Zoarium cup-shaped, poriferous face external, zoarial expansion with only minor flexure. Branches straight, relatively thick (0·16–0·27 mm.), sides on obverse rising rather steeply to a prominent narrow carina with large nodes; nodes with elongate-oval bases. Dissepiments short, straight, about half (0·10 mm.) the thickness of the branches, set well below the general surface of the zoarium. Fenestrules rectangular, a little narrower than the branches, with rounded corners. Zooecial apertures circular, about their own diameter apart, with low, narrow peristomes, not indenting the sides of the fenestrules, $3\frac{1}{2}$–4 to a fenestrule. Zooecial bases subpentagonal (hemi-hexagonal) to subrectangular.

Discussion. The mesh-dimensions of *F. hemispherica* are close to those of several other species, namely *F. stocktonensis* Condra and Elias 1944, *F. cavifera* Shulga-Nesterenko 1941, *F. retiformis* Schlotheim in Shulga-Nesterenko (1941), and *F. modesta* Ulrich 1890. Of these, the first three differ in having more carinal nodes (about 15 in 5 mm.) than *F. hemispherica*. *F. modesta* Ulrich has a less dense branch packing (17–20, as against 21–27), low, rounded carina with small nodes, and zooecial apertures 'almost twice their diameter apart'.

Fenestella oculata M'Coy 1844

Plate 26, fig. 1

Fenestella oculata M'Coy 1844, p. 203.

M'Coy's description. 'Interstices very broad, flattened, rarely branched, obscurely keeled; dissepiments less than one-fourth the thickness of the interstices, regularly placed; fenestrules half the width of the interstices, rectangular, three times as long as wide; pores placed close to the margin, very large, with a thickened margin, which deeply indents the sides of the fenestrule, three between each dissepiment; reverse smooth.'

Material:

1. Holotype NMD XXVIII. 15. i, from 'Carboniferous Slate', Ballynacourty, Dungarvan, Waterford, Eire: probably Tournaisian.
2. Paratype NMD XXVIII. 15. ii, ditto.

Micrometric formulae:

1. Holotype . .	16–18	9–10	15–17	18–19
2. Paratype . .	12–14	8–13	15–17	20–24

Description. The matrix of M'Coy's specimen is a dark-grey irregularly laminated shaly mudstone. There are two fenestellid fragments, both showing the obverse surface; one, 15×15 mm., is heavily recrystallized, obscure, and somewhat compressed; the other, 10×4 mm., is slightly bent, but shows a fairly clear surface. No positive conclusion can be reached as to the form of the zoarium. The larger of the two fragments is slightly flexed, and there is nothing to suggest any departure from the 'normal' form of fenestellid fronds, namely a fan-shaped, cup-shaped, or conical expansion.

Branches thick (0·35–0·50 mm.) and straight, except near points of bifurcation, with steep sides, and a distinct, slightly sinuous, noded carina. Dissepiments short, relatively slender (about 0·20–0·24 mm.). On both specimens some of the dissepiments are set slightly oblique to the meshwork symmetry axes, and are thus aligned across the zoarium so as to give a slanting appearance to the cross-members of the mesh: this is taken to be a secondary distortional effect, and to be without morphological or taxonomic significance. Fenestrules quadrate, rather angular, narrow, the length (0·60–0·75 mm.) usually approximating to or slightly exceeding twice the width (0·27–0·36 mm.). Zooecial apertures large, with prominent peristomes indenting the fenestrule sides, about their own diameter apart (internal diameter 0·07–0·08 mm.; external diameter 0·16–0·19 mm.). Usually two apertures 'occupy' a fenestrule side, with one opposite the insertion-point of the corresponding dissepiment, there being thus three apertures to a fenestrule. Zooecial bases subpentagonal or hemi-hexagonal.

Discussion. It is clear that M'Coy's diagnosis was based on the larger and less well preserved of the two fragments. In this, recrystallization and compression have caused thickening of the branches, which are also pressed together, so that the dissepiments are bent downwards into the matrix. This compression is the cause of the discrepancy between the two branch-density counts, 16–18 for the holotype, 12–14 for the paratype. The smaller fragment, which is almost certainly structurally continuous with the larger one within the matrix, gives a clearer and undistorted view of the mesh, but even here the

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EXPLANATION OF PLATE 24

Figs. 1–3. *Fenestella plebeia* M'Coy. 1, Proximal part of holotype NMD XXIX. 3, showing internal structure of branches, × 30. 2, SM E. 5231, moderately weathered part of obverse showing mature mesh, ×30. 3, SM E. 5231, heavily weathered part of obverse, showing arrangement of zooecial chambers above their bases, ×25.

Fig. 4. *Fenestella hemispherica* M'Coy. SM E. 17841, showing mature mesh, ×25.

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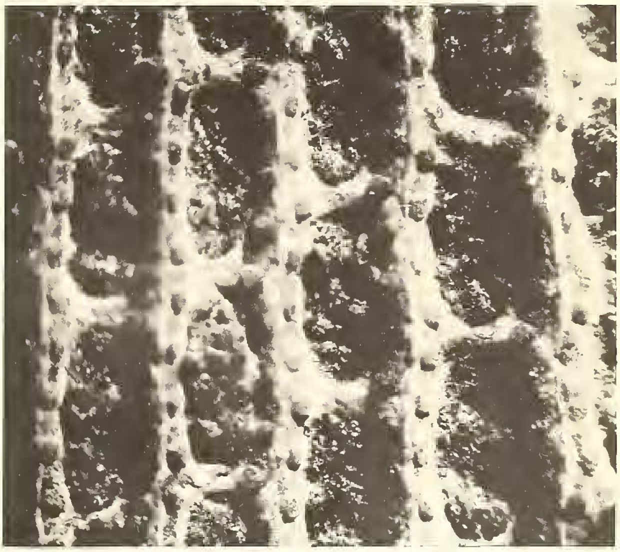

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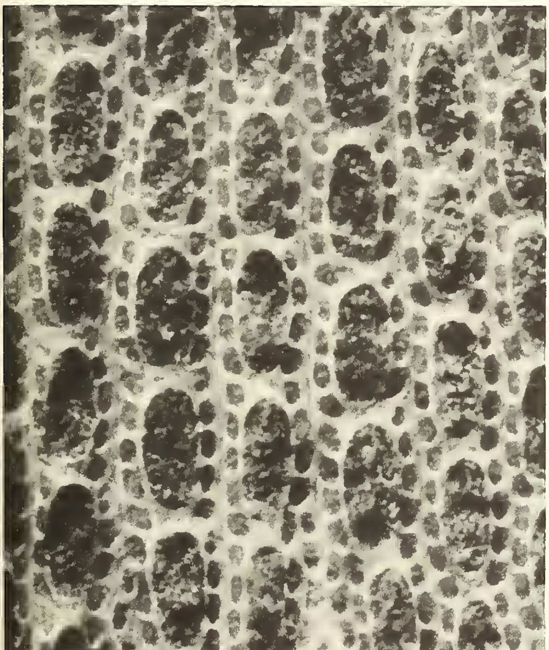

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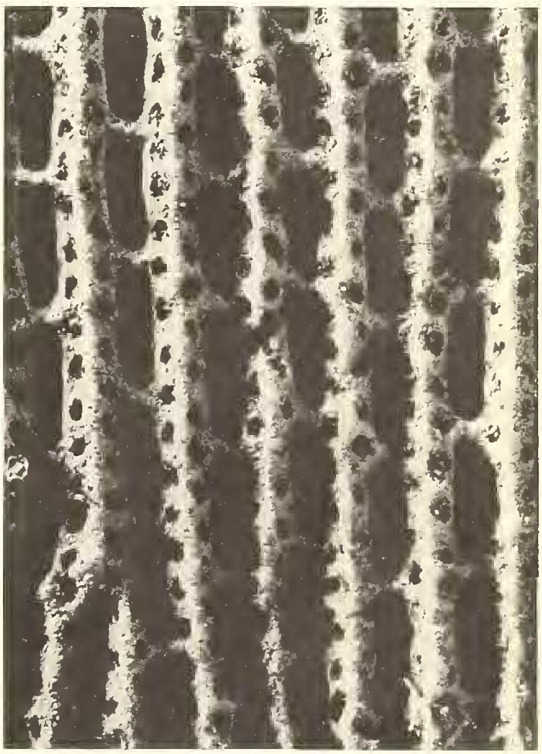


4

MILLER, Carboniferous *Fenestella*

sclerenchymal tissue has recrystallized too much for the external ornamentation to be determined.

The species is superficially close to *F. plebeia*, but differs in the distribution of zooecial apertures and carinal nodes. The mesh elements of *F. oculata* are, in general, stouter than those of *F. plebeia*. Nikiforova (1933*b*) lists the species from the Upper Carboniferous of Samarskaia Luka in the Urals.

Fenestella quadradecimalis M'Coy 1844

Plate 26, fig. 2

Fenestella quadradecimalis M'Coy 1844, p. 204

M'Coy's description. 'Interstices slightly flexuous, thin, irregularly branching; dissepiments thin, distant; fenestrules very large, irregular in shape, pores very numerous, prominent, about fourteen to the length of a fenestrule; reverse finely striated longitudinally.'

Material:

1. Holotype NMD XXVIII. 13, from 'Carboniferous Upper Limestone', Black Lion, Enniskillen, Northern Ireland: probably Viséan.

Micrometric formula:

1. Holotype . .	9–13	$2\frac{1}{2}$–3	21–$22\frac{1}{2}$	3

Description. M'Coy's specimen is roughly triangular, measuring 40×40 mm. It is a proximal fragment of a zoarium but does not include the point of origin or 'root'. At this stage of development of the colony the rate of branch-bifurcation is greater than in the mature or 'stabilized' part, and the mesh is, in consequence, less regular.

Zoarium probably a fan-shaped expansion, rendered rather flexible by the markedly sinuous, widely separated branches, and the short, sometimes slightly obliquely set, dissepiments. Branches relatively slender for the general scale of the mesh (but, compared with other species of *Fenestella*, still moderately thick) 0·27–0·36 mm. Obverse not visible in the unprepared holotype, but in thin-section appears rounded, with a carina carrying small, widely separated nodes. Reverse rounded, with fine longitudinal ribs or striae, five to a branch. Dissepiments short, slender (0·14–0·20 mm.), about half the thickness of the branches or often less. Occasionally, as in the proximal part of the zoarium, slightly oblique. Smooth, without ribs or striations. Fenestrules variable in shape proximally, but generally long and narrow, commonly with one end, at the bifurcation of a branch, pointed, but tending distally towards a long rectangular or roughly coffin-shape (0·50–1·0 mm. wide, 3·0–3·5 mm. long). Zooecial apertures (not seen on the natural surface of the holotype, but revealed locally by abrasion and polishing), small, circular, about their own diameter apart, eleven to fourteen to a fenestrule.

Discussion. M'Coy's figure gives a fair impression of the species, except that the slenderness of the dissepiments is exaggerated. The thick, protruding peristomes figured by M'Coy are not directly visible in the holotype, but have been confirmed by preparation. Comparable species are *F. regalis* Ulrich 1890, *F. undecimalis* Shulga-Nesterenko 1941, and *F. longa* Nekhoroshev 1932, but none of these has the remarkably close zooecial packing of *F. quadradecimalis* (Z/5 22; cf. *F. regalis* 14, *F. undecimalis* 15, *F. longa* 17–20).

Fenestella frutex M'Coy 1844

Plate 25, figs. 1–4

Fenestella frutex M'Coy 1844, p. 201.
Fenestella lyelli Dawson 1878, p. 288.
Fenestella limbata Foerste 1887, p. 83.
Fenestella limbata Foerste; Nikiforova 1926, p. 175.
Fenestella lyelli 'mut.' Dawson; Bell 1929, p. 101.
Fenestella aff. *limbata* Foerste; Likharev 1934, p. 155.
Fenestrellina limbata Foerste; Elias 1937, p. 318.

M'Coy's description. 'Flabelliform; rising from a distinct root or trunk, and suddenly expanding to a nearly circular network; fenestrules broad, usually quadrangular, but rather irregular in size and shape; interstices thick, frequently branching, slightly flexuous, irregular; dissepiments thin, at regular distances; pores very prominent, their own diameter apart, placed much on the sides, so as to indent the margins of the fenestrules deeply; they are placed alternately, usually two to each fenestrule and one at the origin of each dissepiment; about five interstices in the space of one line; reverse with coarse, waving striae.'

Material:

1. Holotype NMD XXVIII. 10, from 'Carboniferous Upper Limestone', Killymeal, Dungannon: probably Upper Viséan.
2. Syntype NMD XXVIII. 9. ii, ditto.
3. Homeotype SM E. 12985, from 'Carboniferous Lower Limestone Series', Auchenmade Quarry, Dalry, Ayrshire, Scotland.
4. Homeotype SM E. 5275, from 'Carboniferous Lower Limestone', Hook Head, Wexford, Eire.

Micrometric formulae:

1. Holotype and syntype .	22–26	21–26	24	20–24
2. Homeotype SM E. 12985	27–31	20–23	26–27	23
3. Homeotype SM E. 5275. i	23–29	18–20	25–26	21–23
cf. *F. limbata* Foerste . .	20–26	19–26	26	15–25
F. limbata Nikiforova .	20–24	22–24	20–24	16–24
F. limbata Nikiforova .	24–26	20–21	24–26	24–26
F. lyelli Bell . . .	22–26	19	21–26	20

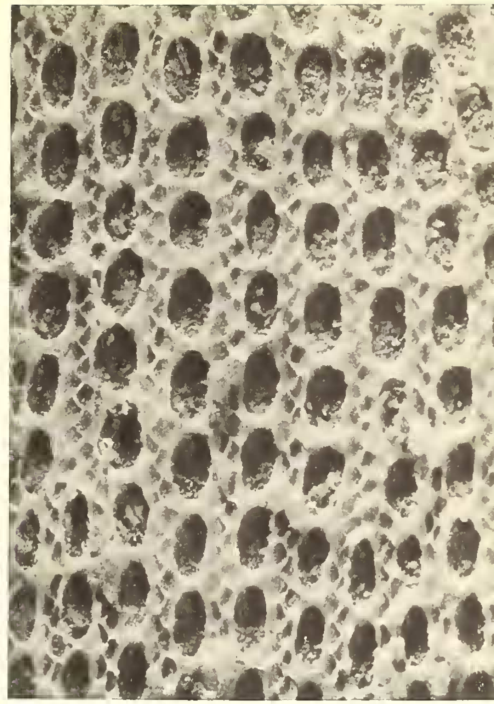
Description. The holotype, a fragment about 10 mm. square, is the reverse of the extreme proximal part of a colony, and has three abnormally thick primary branches growing from an even thicker root-like process. The disposition of the branches in this immature condition is irregular. Moreover, the branches and dissepiments appear to be slightly distorted by the compaction-compression into one plane of a structure originally slightly curved. The syntype is a fragment 9 × 5 mm. of the distal mature part of a zoarium and shows the obverse face.

Zoarium probably a fan-shaped expansion. Branches straight, or very gently curved, moderately thick (0·14–0·20 mm.), steep-sided above, with a prominent narrow carina

EXPLANATION OF PLATE 25

Figs. 1–4. *Fenestella frutex* M'Coy. 1, Holotype NMD XXVIII. 10, showing proximal part of zoarium, with 'root', × 15. 2, SM E. 12985, mesh dissected to show internal structure, × 20. 3, SM E. 12985, mature mesh, obverse, × 20. 4, SM E. 5275, mature mesh, obverse, showing carinal nodes protruding through matrix, × 25.

1



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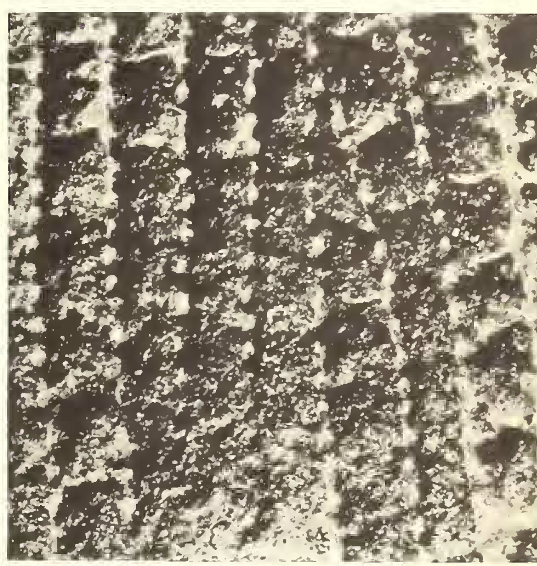

4

MILLER, Carboniferous *Fenestella*

bearing closely set nodes; reverse rounded, with fine longitudinal ribs or striae, 4–6 to a branch. Dissepiments short, narrow (0·04–0·06 mm.), slightly below the general surface-level of the zoarium, often sharply expanded where the region of insertion coincides with a zooecial aperture. Fenestrules quadrate-oval, only slightly wider (0·22–0·30 mm.) than the branches, and 0·33–0·39 mm. long. Zooecial apertures large, circular, set close together on the branches, with thick, prominent, collar-like peristomes, which indent the fenestrule borders. Usually 3 or '3½' apertures along a fenestrule, and almost always one of the apertures is set opposite a dissepiment, so that it appears more prominent than the others. Zooecial bases subpentagonal or hemi-hexagonal, with strongly developed hemisepta set obliquely within the zooecial chambers so as to produce in certain states of weathering an apparently trapezoidal or triangular zooecial base-shape.

Discussion. F. frutex is one of the easiest of M'Coy's species to recognize, mainly on account of the regularity and symmetry of the mesh, and the prominence of the zooecial apertures that lie opposite the ends of dissepiments.

Elias and Condra (1957) place *F. limbata* Foerste, now referred to *F. frutex* M'Coy, in a group with *F. tenax* Ulrich, which is referred to *F. bicellulata* R. Etheridge jun.: '[This] large polyphyletic group includes two conservative long-range species, *F. tenax* and *F. limbata*, and several species and varieties of the comparatively rapidly evolving lineage of *F. mimica*, type-species of the group. . . . The two more conservative stocks of the group, *F. limbata* and *F. tenax*, range from Lower Des Moines [Upper Namurian] to Big Blue [Sakmarian] . . . and from Warsaw [Lower Viséan] to Lower Leonard [Lower Artinskian] respectively, surviving to Permian time without appreciable change.' It is significant that these two very characteristic species should occur in European as well as North American Carboniferous sections. Records of *F. limbata* Foerste, now referred to *F. frutex* M'Coy, are fairly common in studies of Lower Carboniferous rocks of Europe, Turkestan, and North America. In Britain the species occurs in the Viséan Bryozoan Band of Westmorland (Garwood 1912) in a fenestellid faunule of markedly North American aspect, with *Fenestella rectangularis* Condra and Elias as the commonest species, closely followed by *Hemitrypa hibernica* M'Coy.

Fenestella polyporata (Phillips) 1836

Plate 26, figs. 3–4

Retepora polyporata Phillips 1836, pp. 199, 245.
Fenestella polyporata (Phillips); Portlock 1843, p. 323.
Fenestella multiporata M'Coy; M'Coy 1844, p. 203.
Fenestella polyporata (Phillips); Shrubsole 1879, p. 280.
Fenestella polyporata (Phillips); Shrubsole 1881, p. 185.
Fenestella polyporata (Phillips); Nikiforova 1926, p. 179.
Fenestella aff. *polyporata* (Phillips); Nikiforova 1927, p. 251.
Fenestella polyporata (Phillips); Nikiforova 1933*a*, p. 23.
Fenestella ex. gr. *polyporata* (Phillips); Nekhoroshev 1935, p. 69.
Fenestella cf. *polyporata* (*Phillips*); Oakley 1948, p. 88.

Phillips's description. 'Interstices thick; fenestrules large, irregular; pores numerous, small, round. This somewhat resembles retepora cyathiformis [*sic*] Goldfuss ix. 11.'

M'Coy's description of *Fenestella polyporata* (Phillips): 'Interstices thick, rounded (not carinated?), irregularly branched; dissepiments short, thin, placed at irregular distances, fenestrules large, very irregular in size and shape; pores very small, impressed, from five to seven in the length of a fenestrule.'

M'Coy's description of *Fenestella multiporata* M'Coy: 'Foliaceous; interstices thin; sharply keeled, irregularly branched; dissepiments thin, distant, fenestrules large, very elongate, irregular; pores very numerous, small, margins tumid, seven or eight to the length of a fenestrule; reverse regularly striated.'

Material. I believe Phillips's specimen is lost. *Fenestella multiporata* M'Coy is now referred to *Fenestella polyporata* (Phillips), and the holotype of M'Coy's species is here designated as neotype of *F. polyporata* (Phillips).

1. Neotype NMD XXVIII. 9 from 'Carboniferous Upper Limestone', Killymeal, Dungannon, Tyrone, Northern Ireland: probably Upper Viséan.
2. Homeotype SM E. 5244 from 'Carboniferous Limestone', Settle, Yorkshire: Viséan.

Micrometric formulae:

1. Neotype . . .	12–15	4	16–18	?
2. Homeotype . . .	9–10	3–5	15	?
F. polyporata Phillips, Nikiforova 1933*a*	9–12	$4\frac{1}{2}$–6	16	?
F. ex gr. *polyporata* (Phillips): Nekhoroshev 1935	11–12	$4\frac{1}{2}$	$13\frac{1}{2}$–14	?
F. cf. *polyporata* (Phillips): Oakley 1948	14	6	18–20	?

Description. Zoarium probably a limp flexuous expansion. Branches relatively thin (0·22–0·33 mm.), bifurcations frequent (at intervals of about 3 mm.), producing an effect of irregularity; obverse of branches smooth, rounded, with a narrow, indistinct, slightly sinuous carina carrying small, indistinct nodes; reverse finely ribbed or longitudinally striated, eight to twelve ribs on each branch. Dissepiments short, relatively thin (0·11–0·16 mm.), finely ribbed on both sides, the ribs conforming to the long-axis shape of the dissepiment. Fenestrules long, narrow, rectangular, with rounded corners, 2·05–2·25 mm. long, 0·45–0·60 mm. wide. Zooecial apertures large, circular, diameter 0·13 mm., rather less than their own diameter apart, usually 8 or 9 to a fenestrule. Peristomes distinct, narrow, entire. Zooecial bases subpentagonal or compressed hemi-hexagonal. Hemisepta strongly developed and very oblique, giving to the branches in certain states of weathering the appearance of a branch of *Polypora*.

Discussion. There can be little doubt as to the identity of Phillips's and M'Coy's species. The large number of zooecial apertures to a fenestrule is shown clearly in the published figures of both authors (Phillips pl. i, figs. 19, 20; M'Coy pl. xxviii, fig. 9), although the general appearance of the zoarium is equally distorted in the two cases, Phillips exaggerating the irregularity, and M'Coy the regularity, of the branch disposition. Phillips's figure does not show the characteristic thread-like carina.

EXPLANATION OF PLATE 26

Fig. 1. *Fenestella oculata* M'Coy. Paratype NMD XXVIII. 15. ii, part of obverse, × 20.

Fig. 2. *Fenestella quadradecimalis* M'Coy. Holotype NMD XXVIII. 13. partly ground and polished to show features of obverse, ×20.

Figs. 3–4. *Fenestella polyporata* (Phillips). 3, Neotype NMD XXVIII. 9, part of weathered obverse showing gross characters of mesh, ×3. 4, Neotype NMD XXVIII. 9, showing *Polypora*-like appearance when hemisepta are exposed by weathering, ×15.

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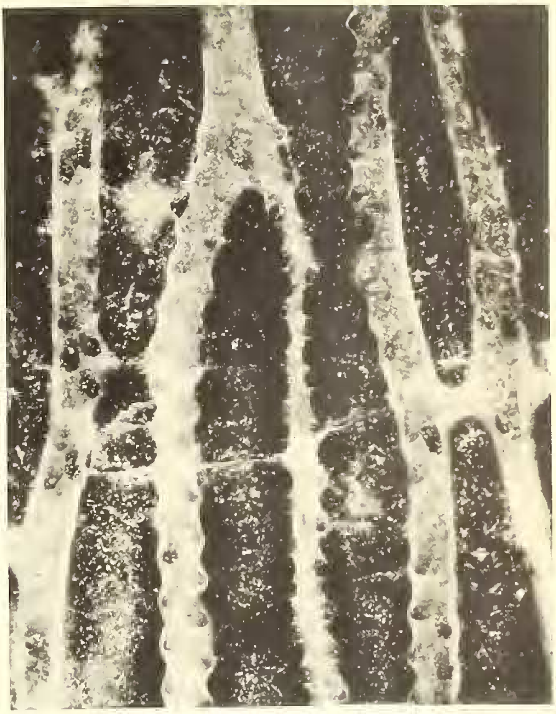

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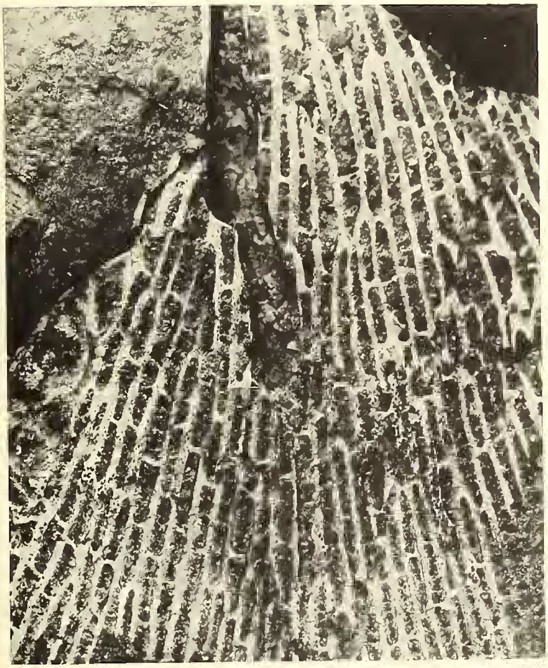

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4

MILLER, Carboniferous *Fenestella*

Fenestella longa Nekhoroshev 1932 has a micrometric formula close to that of *F. polyporata*:

F. polyporata (Phillips) .	9–15	3–5	15–18	?
F. longa Nekhoroshev .	13–15	4–5	17–20	?

It is possible that on re-examination these two may be found conspecific. *F. pseudovirgosa* Nikiforova 1938 also has a similar micrometric formula, but its mesh is much stouter, and its zooecial bases are triangular. The type-material is Viséan. Nikiforova lists *F. polyporata* from the Viséan of the Donetz basin and the Urals, and from the Tournaisian of Turkestan; and a variety—var. *orlovskensis*—from the Middle Carboniferous of the Donetz basin.

Fenestella bicellulata R. Etheridge jun. 1873

Plate 27, fig. 1

Fenestella bicellulata R. Etheridge jun. 1873, p. 101.
Fenestella tenax Ulrich 1888, p. 71.
Fenestella tenax Ulrich; Ulrich 1890, p. 546.
Fenestella cf. *tenax* Ulrich; Nikiforova 1933*a*, p. 15.
Fenestella aff. *tenax* Ulrich; Prantl 1934, p. 231.
Fenestella tenax Ulrich; Condra and Elias 1944, p. 99.
Fenestella cf. *tenax* Ulrich; Oakley 1948, p. 88.
Fenestella submicroporata Shulga-Nesterenko 1952, p. 35.
Fenestella tenax Ulrich; Elias and Condra 1957, p. 106.

Etheridge's description. 'Polyzoarium, probably flattened, expanding. Interstices straight, carinated, occasionally bifurcating, the whole of the carina is occupied by large prominent pores, the openings of which are visible with a strong lens; one pore is placed at the end of each dissepiment, and one between. Dissepiments thin, sub-opposite, and a little arched, not expanding at their junction with the interstices. Fenestrules nearly square, with the margins slightly indented by the cells. Cells, in alternating rows on the margins of the fenestrules, one placed in each angle formed by the junction of the interstices and the dissepiments; a larger cell is placed at each angle of bifurcation of the interstices; all the cells have prominent margins. Non-poriferous face, not known. When highly magnified the foramina are distinctly visible. The characteristic points in this species are the very few cell apertures in a fenestrule, and the regularity with which the interstices are pored.'

Etheridge did not publish a figure of his new species, and his specimen is now presumed lost.

Material:
1. Neotype GSE. 1994, from shale between First and Second Calderwood Limestone, 'Lower Carboniferous Limestone Group', Boghead, East Kilbride, Scotland.

Micrometric formulae:

Neotype	24–27	27–28	27–29	29–31
F. tenax Ulrich 1890 . .	28–30	28–30	27–29	26
F. tenax Ulrich: Nekhoroshev 1926	28–30	22–25	24–26	?
F. tenax Ulrich: Condra and Elias 1944	24–35	25–30	25–31	25–30

Description. Zoarial form unknown. Branches relatively thick (0·10–0·125 mm.), straight, steep-sided above, with a wide, well-defined carina carrying numerous large, high, conical nodes, their bases nearly as large as the zooecial apertures; reverse smooth, rounded, with a distinct zigzag. Dissepiments short, straight, thin (0·05 mm.), faintly ridged on the obverse, smooth and rounded on the reverse. Fenestrules rectangular, appearing almost square in some cases, often with irregular sides due to the protrusion of the zooecial apertures; on the reverse almost circular due to accretion of sclerenchymal tissue and zigzag shape of the branches. Zooecial apertures circular, with narrow peristomes, two to three to a fenestrule, so that rather often one aperture lies at the end of a dissepiment and one in the middle of a fenestrule-side. Zooecial bases obliquely elongate pentagonal.

Discussion. F. bicellulata is an extremely distinctive species, easily recognized by its relatively fine, symmetrical mesh, and large, closely packed carinal nodes. There is little doubt of its conspecificity with *F. tenax* Ulrich, a well-known and widely distributed species in North America and elsewhere.

The neotype is from the Viséan of Scotland. *F. tenax* Ulrich occurs in the Mississippian Warsaw group (Lower Viséan) and the Chester group (Upper Viséan–Lower Namurian), in association with *F. rectangularis* Condra and Elias, *F. serratula* Ulrich, *F. matheri* Condra and Elias, *F. cumingsi* Condra and Elias, *F. multispinosa* Ulrich, and *Archimedes spp.* Almost exactly the same faunule, with the notable exception of *Archimedes* (whose nearest occurrence is in Spitzbergen (Forbes, Harland, and Hughes 1958), occurs in the Viséan Bryozoan Band of north-western England (Garwood 1912, and my unpublished determinations).

Fenestella tuberculo-carinata R. Etheridge jun. 1873

Plate 27, fig. 2

Fenestella tuberculo-carinata R. Etheridge jun. 1873, p. 101.
Fenestella tuberculo-carinata R. Etheridge jun.; Young 1882, p. 182.

Etheridge's description. 'A large number of fragments of a species of *Fenestella* allied to *F. formosa* M'Coy were obtained from shale in connexion with the Hosie Limestone, yet differing sufficiently to be worth recording. The interstices are carinate and occasionally bifurcate, with a large cell-aperture in each angle of bifurcation, as in M'Coy's species. The dissepiments are short and alternate one with the other, but, unlike *F. formosa*, without any trace of cell openings on them. The fenestrules are quadrangular, having a bulging appearance caused by slight undulation of the interstices. The cells, which are very large, with prominent margins, are arranged in alternating series on each side the interstices, three to each side the fenestrule, with very small interspaces between each aperture. Along the keel of the interstices are ranged numerous small, blunt, tubercle-like pores, one at the end of each dissepiment, and three between—that is, one between each pair of obliquely-opposite cell-apertures. On the non-celluliferous aspect, the fenestrules appear quite oval, and the whole aspect smooth and plain. Although somewhat resembling *F. formosa*, this form differs in not having the dissepiments celluliferous, by a less number of cell-apertures to each fenestrule, by a larger number of pores on the keel, and by the nature of the reverse aspect. If better specimens should prove this to be a new species, a good name for it would be that of *Fenestella tuberculo-carinata.*'

Etheridge did not publish a figure of his new species, and his specimen is now presumed lost.

Material. Slide-mount in H.M. Geological Survey collection, number GS 89041, containing nine frag-

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EXPLANATION OF PLATE 27

Fig. 1. *Fenestella bicellulata* R. Etheridge jun. Neotype GSE. 1944, obverse, ×30.
Fig. 2. *Fenestella tuberculo-carinata* R. Etheridge jun. Neotype GS. 89041. O3, obverse, ×30.
Figs. 3–4. *Parafenestella formosa* (M'Coy). 3, Holotype NMD XXIX. 2, obverse, × 20 (the dark band along carina and dissepiments is a weathering effect). 4, Holotype NMD XXIX. 2, oblique view of a dissepiment, showing the dissepimental node (casting its shadow to the 'south-east'), ×70.